THE RELATIONSHIP BETWEEN CORPORA ALLATA AND REPRODUCTIVE ORGANS IN STARVED FEMALE LEUCOPHAEA MADERAE (BLATTARIA)

ARNE SEMB JOHANSSON[1]

Department of Anatomy, University of Colorado School of Medicine, Denver 20, Colorado

It has long been known that hormonal regulation plays an important role in insect reproduction. Aside from the medial neurosecretory cells of the protocerebrum whose action on egg development has been demonstrated in Calliphora (Thomsen, 1952), the corpora allata are necessary for the normal function of the ovary and the accessory sex glands of most insect species investigated (see review: Scharrer, 1953). In the absence of the corpora allata, the oocytes remain in an immature state characteristic of the onset of a given reproductive cycle, and the accessory sex glands stay inactive.

Another important factor in insect reproduction is nutrition. Egg production does not occur in many insect species, when food in adequate quantity and quality is lacking. The question arises, whether the inability of starved insect females to reproduce mature ova constitutes a primary effect, or whether it is due to an influence of inanition on the endocrine system. A previous study indicated that the latter alternative applies to the activity of the corpus allatum of the milkweed bug, *Oncopeltus fasciatus* (Johansson, 1954). In the present paper this problem is studied in a different species belonging to another order of insects.

Material and Methods

Leucophaea maderae is an ovoviviparous cockroach which has been bred in the laboratory for years (*cf.* Scharrer, 1946a, 1946b). Freshly emerged adults which were to serve as donors and hosts, were taken from the stock colonies and isolated in glass jars of pint size. The food consisted of dogchow and apples. The specimens which were used as hosts were starved from the day of emergence and only given water. All specimens were kept at room temperature, *i.e.*, at 26–33° C.

Besides Leucophaea, also females of *Oncopeltus fasciatus,* were used as donors. They were taken from a laboratory colony fed on dried seeds of the milkweed.

Organs to be implanted were dissected out in insect Ringer, taken up in a fine glass capillary connected with a plunger device, and implanted into the abdomen of the host.

The corpora allata of Leucophaea are paired organs. The implantation of one corpus allatum, therefore, means that only half of the organ present in a single individual was used. When three or four corpora allata were implanted, they were taken from two individuals of the same sex and adult age. In Oncopeltus

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the corpus allatum is unpaired. Thus the number of corpora allata implanted in these cases is equivalent to the number of specimens used as donors. Abdominal ganglia of Leucophaea were implanted as controls.

The hosts were killed at various intervals after the implantation and examined. In a few cases they died before examination took place.

Results

In newly emerged females of Leucophaea the ovaries are small, the longest oocytes being about 1 to 1.4 mm in length. No yolk is present. The accessory

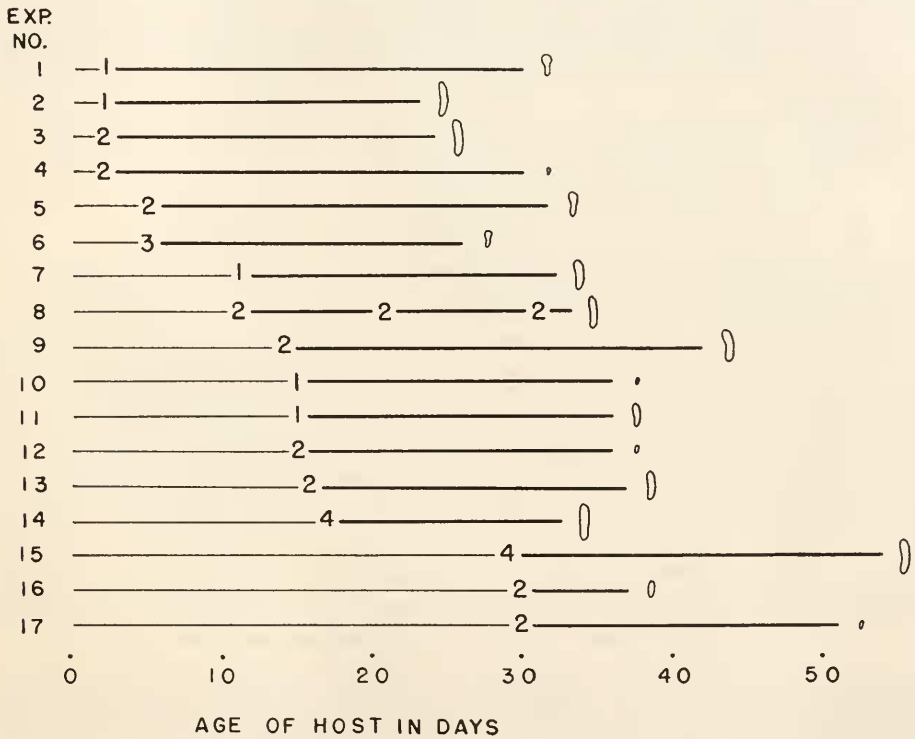

Figure 1. Diagram showing the result of implantations of corpora allata from fed females of *Leucophaea maderae* to starved female hosts. The number of corpora allata implanted and the day of implantation are given in the breaks of the lines. The right end of the heavy lines marks the day on which the host was examined. A schematic drawing in mm. of the largest oocyte observed is shown on the right.

sex glands are inconspicuous and do not show signs of secretion (Scharrer, 1946b). In fed females the oocytes grow and reach their maximal size of about 5 mm. after four to five weeks. During this period yolk is deposited in the oocytes. The accessory glands increase in size and obtain a bluish color due to the accumulation of their secretory product. The corpora allata are necessary, both for the growth of the oocytes and for the secretory activity of the accessory sex glands (Scharrer,

1946b). The corpora allata of Leucophaea do not show any appreciable increase in size during this period of activity.

Starvation of the females of this species prevents egg maturation (Scharrer, 1943). The accessory glands may show some secretory activity, but this does not seem to reach the level characteristic of normally fed specimens. Starved animals could be kept alive up to 74 days, but in none of the 16 specimens examined had the oocytes grown, and no yolk was deposited.

Starvation does not seem to influence the size of the corpora allata of Leucophaea.

Altogether 27 experiments were carried out in which Leucophaea served as donors. In 17 cases corpora allata from normally fed female Leucophaea were used (Fig. 1), whereas in 10 cases corpora allata from fed males were used (Fig. 2). Of the 17 cases with female donors, four did not show any growth of the

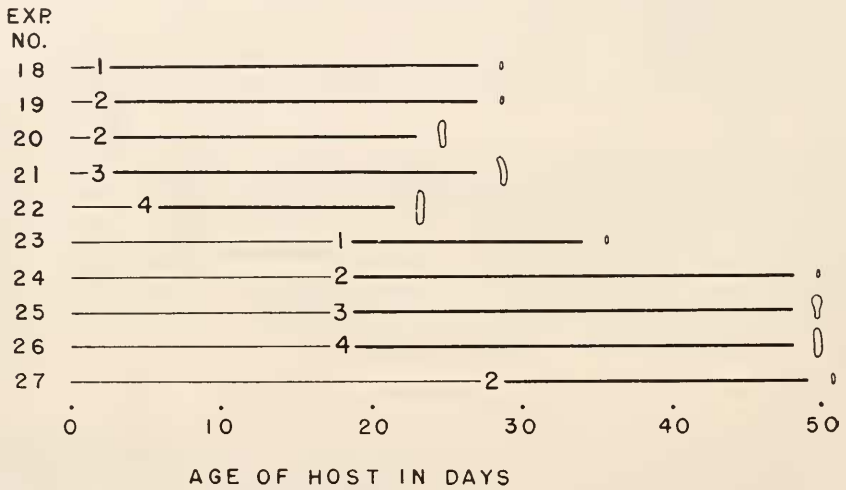

FIGURE 2. Diagram showing the result of implantations of corpora allata from fed male Leucophaea to starved females. For explanation see Figure 1.

ovaries when examined later (Expts. No. 4, 10, 12, 17). In five of the 10 cases with male donors, no development of the ovaries was observed (Expts. No. 18, 19, 23, 24, 27). In the rest of these experiments the implantation of corpora allata into starved hosts resulted in deposition of yolk and growth of the oocytes. As to the negative results, it ought to be mentioned that even in fed females sometimes no eggs develop. The number of grown oocytes observed in these implantation experiments ranged from one (Expts. No. 6, 7) up to normal numbers (Expts. No. 16, 26), *i.e.*, up to 40 (Scharrer, 1946b). In a few cases the shape of the grown oocytes was somewhat irregular. In two cases (Expts. No. 14, 22) eggs were deposited. Premature deposition of eggs is occasionally observed in normal females under laboratory conditions.

The adult age of female donors ranged from one (Expts. No. 7, 13) up to 54 days (Expt. No. 12). In the majority of the cases, the females were from 18 to 38 days old; nearly all had growing oocytes. The female which was 54

days old, had already deposited her eggs when used as a donor. The age of the male donors ranged from 18 to 35 days. It is seen that in the case of female donors even one single corpus allatum from a one-day old specimen can give positive results (Expt. No. 7). It seems that when males are used as donors, two or three corpora allata are necessary to be effective.

Growth of the oocytes took place even when the host had starved up to 30 days before implantation (Expt. No. 16).

The accessory sex glands also responded to the corpus allatum implants. In the experiments in which no growth of the oocytes took place, the accessory sex glands did not seem to increase their activity beyond a level which may be observed also in starved females. In cases with grown oocytes, the accessory sex glands seemed to show an increase in secretory activity beyond the starvation level, and in some cases reached the maximal size characteristic of fed females.

In none of eight experiments, in which one to six corpora allata from fed, egg-laying females of Oncopeltus had been implanted, had the oocytes grown.

In 12 starved females abdominal ganglia from Leucophaea were implanted as controls. No effect was found on the oocytes or the accessory sex glands.

Discussion

It has previously been found that in the milkweed bug, *Oncopeltus fasciatus* implants of physiologically active corpora allata into starved females may induce egg production (Johansson, 1954). The present paper shows that the same is true also in a different species belonging to another order of insects, *i.e.*, in the roach *Leucophaea maderae*. The ovaries of these two species are of different types. Oncopeltus has an acrotrophic type of egg tube, whereas the Blattaria have panoistic ovarioles. In both species starvation apparently prevents egg development by acting on the corpus allatum. In Oncopeltus this is seen in the lack of normal growth of the corpus allatum in starved specimens. In Leucophaea, where the corpora allata do not show any visible growth in fed specimens following emergence, no difference in the size of the corpora allata of fed and starved females could be observed. Also in this species, however, the corpora allata of starved females appear to be physiologically less active than those of fed ones.

No qualitative differences could be found between the action of corpora allata from males and females of Leucophaea, but it seems that quantitative differences exist, the male corpora allata being the less active. The negative results with implants from Oncopeltus may also have a quantitative rather than a qualitative explanation.

The presence of corpora allata has been found necessary for the normal activity of the accessory sex glands. In allatectomized females of Leucophaea the accessory sex glands do not secrete (Scharrer, 1946b). Since these glands in starved females sometimes show a limited secretory activity, it would seem that they have a lower threshold of response to the corpus allatum hormone than the ovaries, and that starvation does not totally prevent the secretion of corpus allatum hormone. A similar phenomenon is observed in Melanoplus where secretion in the oviduct may take place under conditions which prevent yolk production, and Pfeiffer (1945) suggests that the oviducts are able to respond to the corpus allatum hormone before the ovaries react with yolk production.

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Summary

1. In starved females of *Leucophaea maderae* whose ovaries remain immature, egg development can be induced by the implantation of corpora allata from fed donors. Implants from adult males have the same qualitative effect as those from females, but they are by comparison less active. Thus in Leucophaea as well as in Oncopeltus (Johansson, 1954), the inhibition of ovarian development caused by starvation is not a direct effect, but is mediated through the corpora allata.

2. While the oocytes of female Leucophaea, starved from emergence, remain undeveloped, their accessory sex glands may show some measure of secretory activity. The result indicates that these glands whose activity depends on the corpus allatum have a lower threshold of response than the ovaries, and that starvation does not totally prevent the secretion of corpus allatum hormone.

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